Risk, Reward, and the Duration of Feeding Excursions by a Marine Snail

BY

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(5 Text figures)

INTRODUCTION

The intertidal organisms of rocky shores are periodically exposed to two different media, air and water. Each exposure to air interrupts their feeding and other activities, and while exposed they may become overheated or dehydrated. During the exposure, movement is restricted, and birds, mammals, and crabs take advantage of the low tide periods to hunt their immobile prey. Thus, life in the intertidal zone entails many risks that would not be encountered in the subtidal area.

Some intertidal organisms respond to these risks by migrating up and down the shore. Since the exposure time is a function of height above mean lower low water (MLLW; Figure 1), an organism can minimize exposure time by migrating to the lower shore during low tides and returning to the upper shore to feed during high tides. However, each migration is accomplished at high tide, during the potential feeding time. Moves made at the expense of potential food intake clearly have some disadvantages. As an alternative the organism could remain in the feeding zone continuously, or could find crevices or other protected places near the food supply and move to and from these crevices each day.

Thais lamellosa (Gmelin, 1791) and *T. emarginata* (Deshayes, 1839) are rocky shore snails that move up and down the shore. However, these snails do not make regular daily movements with the tides. Based on risks and food supplies, Emlen (1966) predicted that fewer *T. emarginata* would remain on the tops of boulders (where the food was) on warm or sunny days, very stormy days, or days with long tidal exposures. Emlen confirmed these trends for *T. emarginata,* and indicated that movements of *T. lamellosa* are similar.

Emlen's (1966) observations suggest that feeding excursions of *Thais lamellosa* should change in response to changing patterns of risk and reward. At the present study site, on San Juan Island, Washington, the snails feed primarily on the barnacle *Balanus glandula* Darwin, 1854 (Spight, 1981). Barnacles settle throughout the summer, and food quality increases as these barnacles become more numerous and grow. As the summer progresses, low tide exposures become less stressful because the lower tides are higher and occur further from midday. To observe the effects of these temporal changes in risk and reward, I compared feeding behavior during a midsummer and a late summer tidal series.

The following specific questions were asked: (1) are feeding excursions of *Thais lamellosa* more frequent at some stages of the tidal cycle than others, (2) do snails move to hiding places at about the same level as the food supply rather than take longer journeys onto the lower shore, (3) is feeding more frequent in August (when risk is less and reward greater) than in July, and (4) do snails that take longer excursions die sooner? With these questions in mind, daily censuses were taken on a feeding area high in the intertidal zone at Shady Cove, near Friday Harbor, Washington, during two tidal cycles in July and August, 1969.

STUDY AREA AND METHODS

The site, Shady Cove, is about 1 km north of Friday Harbor Laboratories and includes 40 m of shoreline. The steep shore includes only about 5 m of surface between 1.8 m and −0.3 m above MLLW. Most *Thais lamellosa* on this site bore individually numbered tags (Spight, 1974).

Regular censuses were conducted on the whole study area to obtain data for growth and movement studies. Three of these censuses were taken during the activity study period: on 26 June, 11-12 July, and 25 August, 1969.

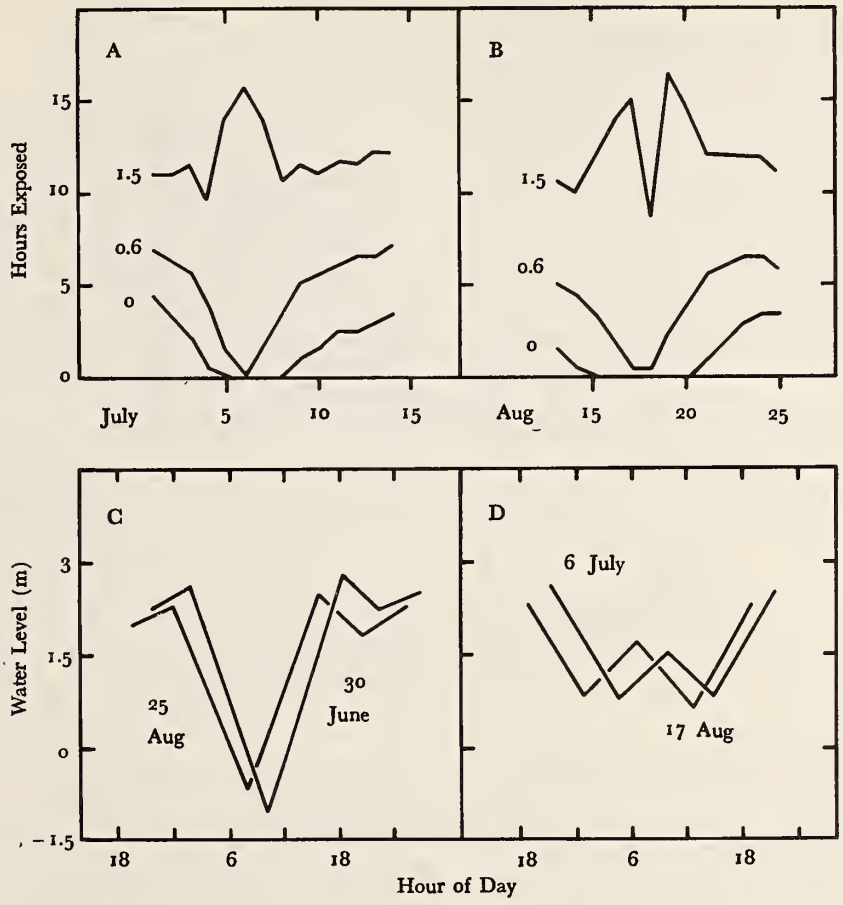

Figure 1

Characteristics of the tidal regime in the Strait of Juan de Fuca, Washington, during the study period, July - August 1969. A and B give the number of hours of exposure on each day at levels of 1.5m, 0.6m and 0m above mean lower low water. C and D give tidal curves for the days with the lowest and highest lower low tides during the study period. Data are from Tison (1969)

Each of these censuses involved a thorough search of the whole study area, which included turning stones and removing snails from crevices. Census data included the tag number of each snail and its location to the nearest 1 m^2 based on a permanent 1 m x 1 m grid marked on the rocks of the whole study area. On the 26 June and 25 August censuses, all snails were left where they were found, and were disturbed only as much as necessary to determine their identities. On the 11 July census, all snails were removed to the laboratory (to be measured for growth studies). These snails were returned on 12 July.

Special censuses were taken July and August 1969, to reveal the searching behavior of the snails. These activity censuses were designed to identify snails that had been actively foraging during the previous immersion period. Snails that were on flat surfaces with barnacles were considered to have been foraging. The locations of all such snails were noted each day, 1-9 and 11 July, and 13-17 and 23-25 August. Snails in crevices were assumed to have been inactive, and their numbers were not taken. Positive locations for these would have been helpful, but it was rarely possible to read the numbers without disturbing the snails, and regular disturbance would probably have affected the behavior of the snails. The activity censuses for 11 July and 25 August were made prior to the regular censuses. The terms "active snails" and "snails on the feeding area" refer only to those snails on the flat surface with barnacles. The "feeding area" does not include the crevices and hiding places which are contiguous with the flat surfaces.

All censuses were taken at low tide, and as the lowest low tide of the day became higher and higher, the accessible area decreased. Only one portion of the Shady Cove site was high enough to have been searched completely on most of the dates (except 6 July and 17 August) and also included a large enough number of snails for meaningful analysis. This area, 3 m deep and 8 m long, and between 0.4 m and 1.8 m above MLLW, is designated the "feeding area." Most activity was on a 3 m x 2 m subarea 0.6 m above MLLW. The less complete observations from other areas were used to determine the fates or sources of snails that moved onto or off the feeding area during the study period.

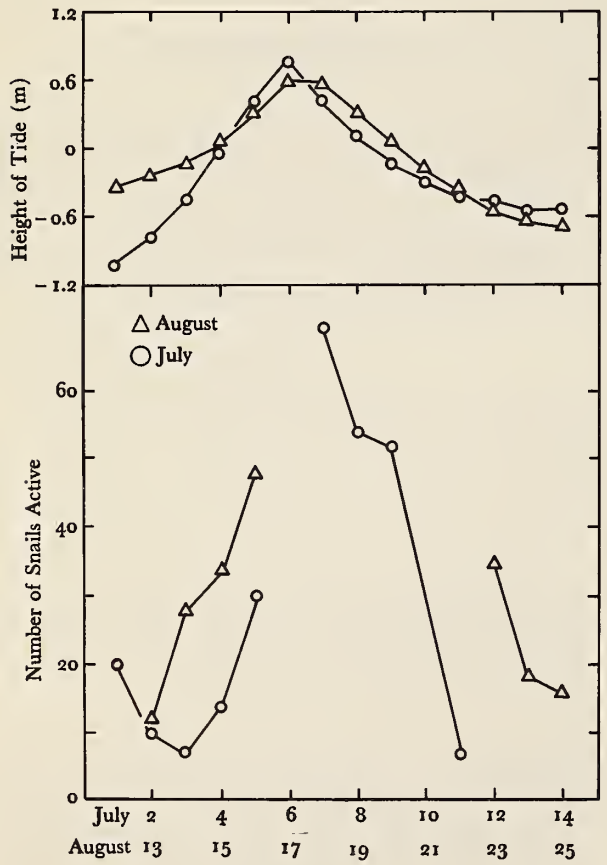

Figure 2

Number of snails on the feeding areas during tidal cycles in July and August 1969. The height of the lowest low tide during each day is plotted in the upper figure. The dates are aligned so that the days of least exposure of each series coincide

RESULTS

Overall Patterns of Activity

Snail activity changed markedly during the tidal cycle. Many more snails were on the feeding areas when tidal excursions were moderate than when they were extreme (Figure 2). However, tidal exposure was not the only factor influencing snail activity. More of the snails were active in August than on comparable tides during July. Also, for a given lower low tide height, many more snails were active when lower low tide heights were increasing on successive days than when they were decreasing (Figure 2).

Behavior of Individual Snails

In total, 159 snails were active (found on the feeding area) on at least one day. However, the average snail was active on only a few of the days. Only 114 snails were found on the feeding area during July, and only 91 during August. Half of the snails were active on only one or two of the 18 census days (82 of 159 snails; Figure 3). Snails that were active during one period were usually inactive during the other period. Of the 159 snails, 127 had been tagged at the beginning of the study period and were still alive at the end. Most of these (86 of 127) were seen on the feeding area during only one of the two periods. Although 56 snails spent three or more days on the feeding area during at least one of the two periods, only 11 snails were active on 3 days during both periods.

Individual feeding excursions were generally short. Only half of the snails (74 of 159) were up on the feeding area on two or more consecutive days, although some remained as long as 5 days. Altogether, there were 4 periods of consecutive daily censuses, each lasting from 3 to 5 days (Figure 2). Even though these periods were short, many snails appeared to make more than one trip (from 4% over 3 days to 21% over 5 days). Actual feeding excursions were undoubtedly longer than the censuses indicate, because it was not possible to take censuses when lower low tides were highest and because some snails on the feeding area were overlooked.

Snails that were not stranded on the feeding areas at low tide must have returned to the lower shore or to nearby crevices before the end of the immersion period. The daily censuses did not include snails in the crevices, and therefore the locations of the secreted snails are not known for most census days. However, the locations of most snails are known for 26 June, 11 July, and 25 August

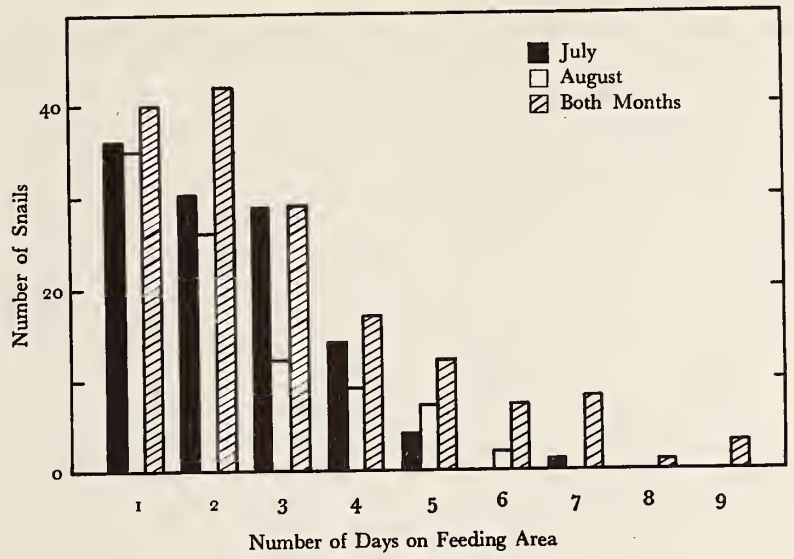

Figure 3

Number of days spent on the feeding area by 159 snails during the July and August, 1969, observation periods, and the total days spent by individual snails during both months

(the beginning and ending of the census periods). These locations can be used to determine how many snails moved vertically. Only 16 of 99 snails (114 less 15 deaths before 11 July) were on the lower shore at the beginning and again at the end of the July census period, while 39 snails made one vertical migration (at the beginning or the end of the period). The remaining 44 snails were on the feeding area or in crevices adjacent to it on both 26 June and 11 July. Observations for the August period are similar (19 snails moved up and down, 30 moved one way, and 31 remained up from 11 July to 25 August; 11 of 91 snails died before 25 August). Therefore, the snails move to and from nearby crevices much more often than they move up and down the shore. Foraging itself may be more frequent than indicated by the censuses because the censuses were taken at low tides and snails may complete foraging trips to and from crevices within each immersion period. However, the censuses do reveal the relative roles of movements to crevices and to the lower shore in the snails' overall behavior pattern.

The snails do make vertical movements frequently. Many of the snails that were seen on the feeding area during only one of the two periods moved up or down the shore. For the August series, 45 new snails moved onto the feeding area; 18 of these moved from the lower shore, and 6 came from elsewhere on the upper shore. Similarly, 50 snails left the area after July, with 20 of these moving lower on the shore and 13 leaving for other feeding areas. All of the snails collected on 11 July were taken to the laboratory, and later returned to a crevice at the base of the feeding area. Of the 159 snails from the feeding area, 74 were released in this crevice on July 11, and 40 of these later moved up the shore and into the feeding area.

Consequences of Feeding Activity

Snails on the upper shore are exposed to physical stresses for long periods when the tide is low (Figure 1). Since these stresses are a major mortality factor (Spight, 1982), snails making extended feeding trips could well have higher death rates than other snails. Censuses were taken over the entire study area until 1973. These data can be used to identify both long- and short-run fates of the feeding snails (Spight, 1972, 1974). Over the short run, results are opposite those expected; through April 1970, survival was somewhat greater among snails that spent more time in the feeding area (Figure 4). Over the long run, results conform to expectation: snails that spent less time on the upper shore feeding areas during these

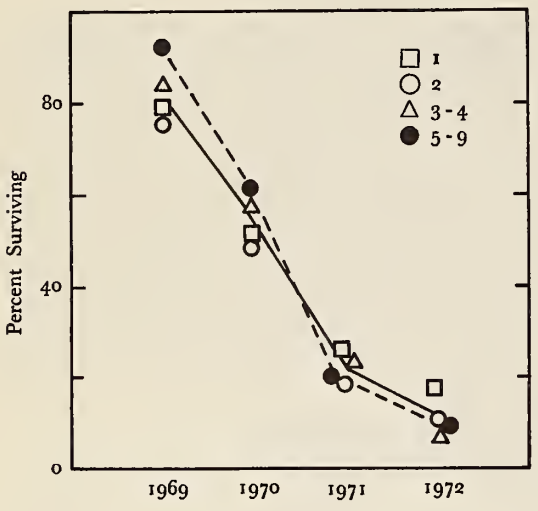

Figure 4

Survival of snails that fed for different amounts of time during July and August, 1969, observation periods. The solid line is the survival for all snails; the dashed line is the survival for the 5-9 day snails

two census periods lived somewhat longer. However, these long-run differences are small and undoubtedly reflect behavior after this study was completed.

DISCUSSION

Each individual snail is faced with a major dilemma: feeding rate can be maximized by staying on the high shore, and risks can be minimized by staying on the low shore. The risks are not trivial; physical stresses are a major cause of death for the Shady Cove snails (Spight, 1982), and moving up the shore into a zone of higher stress bears clear consequences. Likewise, the rewards are often slim. Barnacles are sparse and through much of the year the snails stand to gain little by searching for food (Spight, 1981). Searching and feeding are both time-consuming processes; drilling and feeding require some 2-8 hours per barnacle, and even when allotted a dense barnacle supply under relatively protected field conditions, snails can consume only about 2 barnacles per day (Connell, 1970; Emlen, 1966). Near Friday Harbor, *Balanus glandula* and *B. cariosus* (Pallas, 1788) reach a peak combined density of only about 3/cm^2 (Connell, 1970) between early June and late July (Spight, 1981). The barnacles gradually disappear from the shore during the summer and fall, and few remain by the time the snails become active in the spring. Despite rapid growth, few of these barnacles live long enough to reach sizes preferred by the snails. With this poor food supply, snails can ill afford to spend potential feeding time merely avoiding stresses. Feeding becomes more risky as the season progresses, because the snails eat the low shore barnacles first, and gradually work their way up the shore as the fall approaches. By spring, the safe lower shore and the remaining upper shore barnacles are often several meters apart.

The complex tidal cycle for the Friday Harbor area adds another dimension to the problem. The behavior of some intertidal organisms is often adjusted closely to such complexities (Enright, 1972), and one would expect the snails to track the tidal changes closely to minimize stresses. When the lower low tide is highest, the top of the barnacle zone (1.5 to 1.8 m above MLLW) emerges twice a day (Figure 1D), and the dry periods are long (Figure 1A, B). During the lowest low tides, even the mid-shore is exposed for 5 hours or more for several days in succession, and in summer often during the warmest part of the day. These long exposures are followed by the longest immersion periods of the tidal cycle; when the tides are at the extremes there are effectively only two tides per day (Figure 1C). The snails are also exposed progressively later and then earlier in the day as the year proceeds. Near Friday Harbor, the lowest low tides of the year are at mid-day during the warm part of the year and in the middle of the night during the coldest part of the year. During this study, lower low tide times progressed from mid-day in July to early morning in August (Figure 5). Weather effects are superimposed on the relatively predictable tides; a very long tidal exposure could take place on a cool foggy day that presents little stress to the snails, or on a hot dry day that presents very significant stress.

If risk varies so markedly over the tidal cycle, then the optimum behavior for the snail probably varies as well. The risk attending a trip from the lower to the upper intertidal zone is affected by the distance to move, the weather, and the time of exposure, while the reward reflects the density and size of available food items. When the snail often cannot find a barnacle and finish drilling and feeding during a single immersion, risks from predators and physical stresses may outweigh potential gains from foraging. Emlen (1966) has hypothesized that an individual *Thais emarginata* will leave more offspring if it sits and starves when feeding entails high risks, even though food is "available."

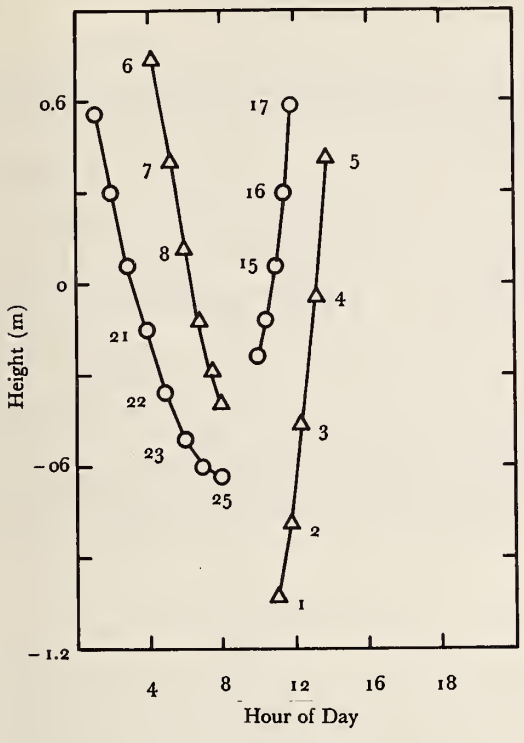

Figure 5

Time and height of lower low tides on 1 - 11 July (△) and 13 - 25 August, 1969 (○), in the Strait of Juan de Fuca, Washington, from Tison (1969). The numbers are dates

How do the snails solve this problem? Firstly, more snails make feeding excursions during less stressful phases of the tidal cycle (Figure 2). Few snails are active when the tides are lowest, but many are active when the lower low tides are highest. However, activity lags behind the tides. For a given tidal excursion, activity is higher when lower low tide heights are decreasing than when they are increasing (Figure 2). In part, this may reflect the timing of the tides; heights are decreasing when tides are in the morning and weather is often cool and foggy, while heights are increasing when tides are in the afternoon, and the air is often warm and clear (Figure 5). The lags suggest that the snails adjust their activity to actual stresses rather than anticipating the tidal cycle. *Thais emarginata* also responds to actual stresses (Emlen, 1966).

Secondly, feeding excursions are more frequent during less stressful seasons. More snails made feeding excursions in August than in July (Figure 2). The tidal cycles during these two months differed in both risks and rewards. The July series fell more toward the middle of the day (Figure 5). On lower low tides of July, water was rapidly evaporated from the intertidal surface and temperature stress must have been significant. The July study period also fell before barnacles reached maximum density. In July, almost all barnacles were small and newly settled. A month later, air temperatures were lower, the tides fell at a less stressful time of the day, and the larger barnacles provided a much more substantial return for drilling and searching effort. Appropriately, many more snails were on the feeding areas during all phases of the census period (Figure 2).

Thirdly, the snails retreat to crevices adjacent to the feeding areas rather than to the lower shore. Active snails typically made short trips into the feeding area, often lasting several days, followed by short trips to nearby crevices. Many snails did make long vertical migrations, but fewer than 25% of them actually made complete round trips from and back to the lower shore during either census period.

The most outstanding aspect of the behavior of these snails is the prevalence of individual differences. Only 41 of 127 snails were active during both census periods. Half of the snails were active on only one or two days of the 8-10 day census periods and activity was scattered throughout both census periods. A few snails moved up and down the shore, a few left for other feeding areas, and others spent their inactive periods in crevices adjacent to the feeding area. Although some days were better than others for activity – based on snail numbers – no day was good enough to draw out a majority of the nearby snails.

Individuals who appeared to take greater risks also survived better in the short run. The benefits of feeding probably outweighed the risks of activity because the snails were in poor condition after several months of low food intake. In the long run, the more active snails did not survive as long (Figure 4). However, it would be premature to interpret this slight long-term difference.

SUMMARY

Thais lamellosa often forages on the upper levels of rocky intertidal shores, and it increases its risk of death from physical stresses and some predators when it does. Studies during two tidal series revealed more frequent foraging as risks decreased and food supplies increased. Snails were more active on the less stressful days of each tidal series and on comparable days of the less stressful tidal series. Some snails spent their inactive time on the lower shore, but most retreated to crevices near the feeding area; thus, they did

not make daily trips up and down the shore. The net movement was downshore for the lowest low tides of each two-week series, but only 40% of the active snails made a downshore move. Individual differences formed the most prominent aspect of the behavior of these snails. Despite higher stresses in the feeding area, snails spending more time on the upshore feeding areas did not have higher death rates than less active snails.

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Literature Cited

Connell, Joseph H.
1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecol. Monogr. 40: 49 - 78

Emlen, John Merritt
1966. Time, energy and risk in two species of carnivorous gastropods. Thesis, Univ. Wash., Seattle, 126 pp.; 18 figs.

Enright, J. T.
1972. A virtuoso isopod: circa-lunar rhythms and their tidal fine structure. Journ. Comp. Physiol. 77: 141-162

Spight, Tom M.
1972. Patterns of change in adjacent populations of an intertidal snail, *Thais lamellosa*. Ph. D. Thesis, Univ. Washingt., Seattle; 308 pp.; 48 figs.
1974. Sizes of populations of a marine snail. Ecology 55: 712 - 729
1981. Settlement patterns of two rocky shore barnacles. Ecosynthesis 1: 93 - 120
1982. Population sizes of two marine snails with a changing food supply. Journ. Exp. Biol. Ecol. 57: (in press)

Tison, J. C., Jr.
1969. Tide tables, high and low water predictions, 1969, West Coast North and South America including the Hawaiian Islands. U. S. Dept. Commerce Coast and Geod. Surv., Washington, D. C., 224 pp.